

DAILY AND SEASONAL MOVEMENTS AND HABITAT USE BY FEMALE ROCKY MOUNTAIN ELK AND MULE DEER

ALAN A. AGER,* BRUCE K. JOHNSON, JOHN W. KERN, AND JOHN G. KIE

*United States Forest Service, Umatilla National Forest, 2517 Southwest Hailey Avenue,
Pendleton, OR 97801, USA (AAA)*

Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA (BKJ)

Kern Statistical Services, 415 Northwest Robert Street, Pullman, WA 99163, USA (JWK)

*United States Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande,
OR 97850, USA (JGK)*

We examined movements and habitat use by female Rocky Mountain elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) using a large telemetry data set collected over 6 years at the Starkey Experimental Forest and Range in northeastern Oregon. The analysis contrasted hourly movements of elk and deer within the mosaic of vegetation and landforms at Starkey with daily and seasonal demands for forage, security, and other resources. Telemetry data from 15 April to 14 November, 1991–1996, were stratified into 30-day intervals and tested for daily cycles relative to habitat use and movements. Both elk and deer exhibited strong daily and seasonal patterns of movements and habitat use. Daily cycles were most pronounced during spring and autumn, were composed of crepuscular and intraday habitat transitions, and were more pronounced for elk than for deer. Although crepuscular transitions were accompanied by sharp increases in velocity, intraday changes in habitat were not. The results add considerable detail to previous studies that sampled only limited hours of the day and seasons of the year. The findings have significance for modeling efforts that attempt to replicate animal behavior on diverse landscapes.

Key words: animal velocity, *Cervus elaphus*, daily movements, mule deer, *Odocoileus hemionus*, Rocky Mountain elk, seasonal movements, telemetry

The analysis and description of animal habitat use and movements is a function of spatial and temporal scale, making it a challenge to quantify animal behavior in a way that permits building and applying habitat-relationship models (Johnson 1980; Morris 1992). Understanding behavior of ungulates at multiple scales is fundamental to testing hypotheses regarding forage competition, effects of herbivory, and predator–prey interactions (Gross et al. 1995). Previous studies have described large-scale patterns of habitat use by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*)—Craighead et al. 1973; Johnson et al. 2000;

Mackie 1970). More detailed studies have examined bite-level foraging dynamics at the patch or sward scale (Focardi et al. 1996; Gross et al. 1995) and diel activity cycles (Beier and McCullough 1990; Collins and Urness 1983; Collins et al. 1978; Green and Bear 1990). However, integrated studies of movements by individuals and broad-scale use of habitats by populations are rare. We know of no detailed studies of the complex diel and seasonal cycles of behavior by elk and mule deer (Collins et al. 1978; Green and Bear 1990) in the context of landscape-scale patterns of habitat selection (Johnson et al. 2000) and movements (Brillinger et al. 2001, 2002, in press). Examining ungulate behavior across multiple

* Correspondent: aager@fs.fed.us

TABLE 1.—Summary of radiocollared mule deer and elk monitored at the Starkey Experimental Forest and Range, northeast Oregon, 1991–1996.

	1991	1992	1993	1994	1995	1996
Starting date	1 June	1 Aug.	7 May	15 Apr.	15 Apr.	2 May
Ending date	14 Nov.	14 Nov.	14 Nov.	14 Nov.	31 Oct.	31 Oct.
Total number of days ^a	150	102	142	187	172	163
Number of elk	32	22	33	53	38	59
Elk locations	18,759	24,908	71,386	61,299	38,649	72,863
Number of mule deer	8	10	13	33	30	18
Deer locations	5,148	7,883	18,887	41,028	29,961	14,614

^a Total number of days per year is less than the interval between the starting and ending dates due to intermittent periods of maintenance work on the telemetry system.

scales leads to an understanding of how these large, highly mobile species navigate through heterogeneous landscapes in space and time in response to forage phenology, photoperiod, physiological needs, thermal comfort, and disturbance (Coe et al. 2001; Irwin and Peek 1983; Johnson et al. 2000).

We analyzed the daily and seasonal dynamics of movements and habitat use by adult female mule deer and elk using data from >400,000 locations collected over 6 years from the United States Forest Service Starkey Experimental Forest and Range (Starkey) in northeastern Oregon (Rowland et al. 1997). We fit periodic functions to hourly use of habitat variables to quantify daily and seasonal patterns of movement and habitat use of the 2 species. Specifically, we were interested in identifying the spatial and temporal scale at which patterns of habitat use for elk and deer are manifested in diel movements. The findings are significant in building mechanistic foraging models to study interspecific competition for forage (Coe et al. 2001; Johnson et al. 1996) and the effects of large herbivores on forest and range ecosystems (Hobbs 1996; Jorritmsa et al. 1999; Kay and Bartos 2000; Kienast et al. 1999; Pastor and Naiman 1992; Putman 1996; Riggs et al. 2000). Our results also demonstrate how our habitat quality for these species is highly dependent on spatial and temporal scales, a result that has broad implications for other studies using telemetry.

MATERIALS AND METHODS

Starkey covers 101 km² of the Wallowa Whitman National Forest (45°15'N, 118°37'W), 35 km SW of La Grande, Oregon. Our study area was enclosed with a 2.4-m-high woven-wire fence (Bryant et al. 1993) and has been used for studies on Rocky Mountain elk, mule deer, and cattle since 1989 (Rowland et al. 1997). Starkey contained habitat for elk and mule deer typical of summer range conditions in the Blue Mountains. A network of drainages in the project area created a complex and varied topography. Vegetation at Starkey was a mosaic of coniferous forests, shrublands, wet meadows, and grasslands. Traffic levels, recreational activities (including hunting), cattle grazing, and timber management were representative of adjacent public lands. About 500 cow–calf pairs of domestic cattle grazed Starkey on a deferred rotation system through 4 pastures within the study area between 15 June and 15 October (Coe et al. 2001). Details of the study area and facilities are available elsewhere (Noyes et al. 1996; Rowland et al. 1997; Wisdom et al. 1993).

Animal locations and habitat data.—Animal locations were determined by an automated telemetry system using retransmitted LORAN-C radionavigation signals (Dana et al. 1989; Findholt et al. 1996; Johnson et al. 2000; Rowland et al. 1997). We radiocollared adult female elk and mule deer and monitored their distributions between April and November for the years 1991–1996 (Table 1). All animals were handled in accordance with protocols approved by an established Institutional Animal Care and Use Committee (Wisdom et al. 1993). Starting and ending dates and total days of monitoring varied each year due to weather and logistics of the

TABLE 2.—Habitat variables analyzed for daily and seasonal patterns of habitat use by elk and mule deer in the Main Area, Starkey Experimental Forest and Range, northeast Oregon.^a

Variable (unit)	Source	Minimum	Maximum	\bar{X}
Canopy closure of trees >12 cm diameter at breast height (%)	1:12,000 Color aerial photos, 1996	0	95	29
Distance to hiding cover (m)	GIS	0	1,018	102
Distance to open road (m)	GIS	0	2,419	638
Cosine aspect (radians)	USGS 30-m DEM	-1	1	0.07
Sine aspect (radians)	USGS 30-m DEM	-1	1	0.07
Distance to stream (m)	GIS	0	525	274
Convexity (m)	USGS DEM	488	506	500
Slope (%)	USGS DEM	0	84	18
Herbage (kg/ha)	Johnson et al. (2000)	0	2,464	371
Distance to closed road (m)	GIS	0	2,916	452

^a GIS, geographic information system; USGS, United States Geological Service; DEM, digital elevation model.

telemetry system (Table 1). We used a total of 144 elk and 58 deer (Table 1) from the main study area (77.6 km²), where about 430 adult elk and 270 adult mule deer were present during the monitoring period (Noyes et al. 1996; Rowland et al. 1997). Each elk was monitored on average for 1.6 years over the 6-year period, and each deer was monitored for about 1.9 years. Locations were assigned to Universal Transverse Mercator coordinates of associated 30 by 30-m pixels containing habitat information stored in a geographic information system. Locations had a mean error of 53 m \pm 5.9 SE (Findholt et al. 1996) and were corrected with a spatially explicit algorithm for differences in the rate at which telemetry locations were successfully obtained (Johnson et al. 1998).

The main study area at Starkey was 3–4 times larger than typical summer home ranges of elk in the Blue Mountains (20–29 km²—Leckenby 1984), providing study animals with large-scale habitat choices commensurate with free-ranging herds. Densities of adult elk (5.6–6.8 elk/km²) and deer (2.8–3.6 deer/km²) in the study area were similar to those on adjacent public lands (Johnson et al. 2000).

Animal locations obtained during elk rifle-hunting seasons were excluded from analysis after it was found that daily patterns of habitat use and velocities were significantly different during these periods compared with the 2-week period preceding each hunt (A. A. Ager, in litt.). A total of 36,502 observations on elk and 21,449 on deer were deleted during 136 days of elk hunting. Data were not removed for 53 days of deer

rifle hunts, during which average hunter density was less than 0.04 hunters/km². Analyses of these data showed little or no apparent change in animal velocities and habitat use compared with a period of 2 weeks before the hunt.

Habitat data included 10 variables (Table 2) that were selected based on their significance in resource-selection models developed with Starkey data (Coe et al. 2001; Johnson et al. 2000; Rowland et al. 1998, 2000). Aspect data were transformed with sine and cosine functions to measure east–west (sine) and north–south (cosine) aspects (Johnson et al. 2000). Convexity was calculated as the difference in elevation of the home pixel from the mean of the 3-by-3 pixel neighborhood plus a constant of 500 (K. Kvamme, in litt.) and used to describe terrain in terms of ridge and valley morphology. Values >500 indicated convex (ridge) and <500 indicated concave (valley) landforms. Distance to hiding cover was defined as the distance to the nearest stand with >40% canopy closure (Johnson et al. 2000). Forage production data (hereafter herbage) were obtained from Johnson et al. (2000). We included both the distances to open and closed roads in the project area to highlight the effect of traffic. Roads were not stratified into different levels of traffic as in Johnson et al. (2000) because of numerous study constraints. Roads classified as closed were open to administrative traffic and on average received <1 vehicle/month.

Statistical analysis.—Locations for each animal were assigned to twenty-four 1-h periods and seven 1-month intervals between 15 April and 14 November. For each hour–month interval, the

mean sample size was 1,659 locations/h (range, 664–3,144) for elk and 678 locations/h (range, 283–1,168) for mule deer for the 6-year period. The number of animals in each hour–month interval ranged from 51–207 for elk and 31–102 for deer. The 7 intervals were not equally represented among years due to a number of factors, including different starting and ending dates each year, performance of the telemetry system, and number of radiocollars monitored (Table 1). We treated animals as sampling units to avoid pseudoreplication (Otis and White 1999). Thus, locations from individual animals monitored in multiple years were pooled across years.

For each animal, we calculated velocity (m/min) between successive locations by dividing horizontal distance moved by elapsed time. Slope of movement was calculated as the difference in elevation between successive locations divided by horizontal distance moved, expressed as a percentage. We assigned the velocity and slope of movement to the hour nearest the midpoint of the time interval during which the movement occurred. Before velocity analysis, observations were deleted if elapsed time between successive locations was <5 min or >240 min between successive locations. Shorter elapsed times (<5 min) yielded velocities that were positively biased because of the random location error in the telemetry system. Velocities determined at longer elapsed times were negatively biased as a result of undetected movements between observations. Sample sizes for velocity variables were reduced approximately 15% (20,733 deer and 41,781 elk locations). The mean elapsed time between observations used for velocity calculations was 103 min for deer and 92 min for elk.

For each monthly interval, we examined habitat and movement variables for daily patterns by fitting sine and cosine functions at 6-, 8-, 12-, and 24-h cycles (Diggle 1990). The regression coefficients calculated for each variable were accumulated and averaged across animals to obtain estimates of between-animal variance in regression coefficients within an interval. The general form of the model was

$$Y_{\text{est}} = B_0 + B_1 \cos(\omega t) + B_2 \sin(\omega t) \\ + B_3 \cos(2\omega t) + B_4 \sin(2\omega t) \\ + B_5 \cos(3\omega t) + B_6 \sin(3\omega t) \\ + B_7 \cos(4\omega t) + B_8 \sin(4\omega t),$$

where Y_{est} = estimated value of the variable, $\omega = (2\pi)/24$ with π expressed in radians, and t = time in hours. Significance in any of the coefficients B_1 – B_8 indicated cyclical trends in the data. All models were fitted with PROC GENMOD software (SAS Institute Inc. 1994). Overall coefficients were calculated as the average of coefficients for individual animals. Test statistics were computed as the average coefficient divided by SE and compared with the standard normal Z to test for significance with $d.f.$ equal to the number of animals per period. We report results of regressions for periods 1, 3, 5, and 7 after finding that results for the other periods were intermediate from the adjacent periods and thus contained little additional information.

We tested for differences among monthly intervals for each habitat and movement variable at specific hours (0000, 0400, 0800, 1200, and 2000 h) using a sequential Bonferroni multiple comparisons test (Rice 1989), with an overall error rate of 0.05 for each comparison. We also calculated an average, within-interval SD pooled across the 7 monthly intervals. These SD values were used to plot 95% confidence intervals about the grand means.

RESULTS

Daily patterns for elk.—Regression models of elk daily cycles generally had low r^2 values (range, 0.0–0.70; $\bar{X} = 0.23$), even though all habitat variables had ≥ 1 significant regression coefficient (Table 3). Elk exhibited significant 24- or 12-h cycles for nearly all habitat variables and intervals (Table 3), and terms for many 8- and 6-h cycles were also significant. Smaller r^2 values were obtained for midsummer intervals (3–5) compared with those obtained earlier and later (Table 3), suggesting weaker diel cycles compared with the other seasons. Elk exhibited pronounced 24-h cycles with crepuscular transitions for canopy cover, distance to hiding cover, cosine of aspect (Figs. 1A–C), herbage, and distance to open roads (Figs. 2A and 2B). Multiple comparisons showed higher use of forest canopy, greater distance to hiding cover, herbage, and greater distance to open roads ($P < 0.05$, $d.f. = 354$) during daytime than at night for all 7 monthly intervals. Daytime

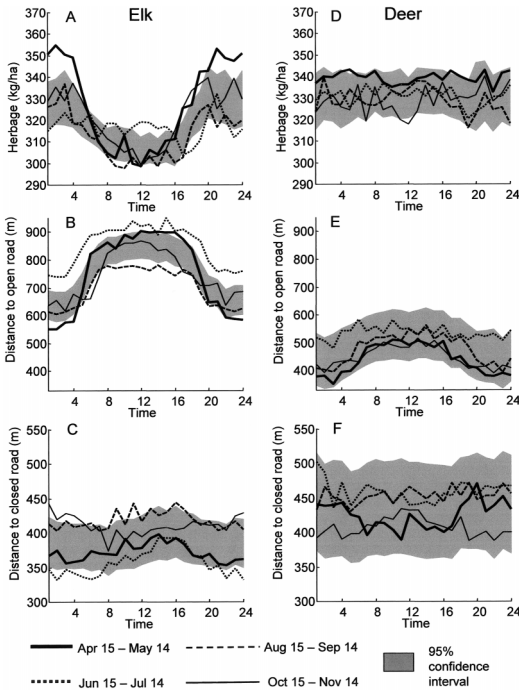


FIG. 2.—Means of habitat variables herbage production, distance to open road, and distance to closed road by hour-month intervals for elk (left column) and deer (right column). See Fig. 1 for additional explanation.

24-h cycles (Figs. 1A–C, 2A, and 2B), slope, sine of aspect, convexity, and distance to stream (Figs. 3C and 4A–C) showed asymmetrical and irregular cycles that exhibited daytime and, in some cases, crepuscular transitions as well. Daytime transitions of these variables were made at relatively low velocity (Fig. 3A), in contrast to high velocities that accompanied major crepuscular changes found in canopy, distance to roads, and cosine of aspect. Daily pattern in sine of aspect (Fig. 4A) showed a steady trend toward more easterly aspects throughout the day, with a rapid transition at dusk back to westerly aspects. From the variables slope of movement, sine of aspect, convexity, slope, and distance to streams, it was possible to discern a morning versus afternoon pattern of habitat use. During morning hours, movements were uphill (Fig. 3B), toward more convex to-

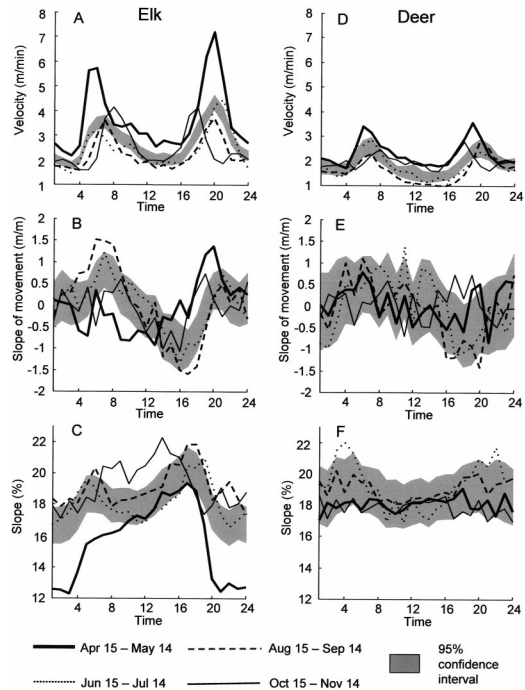


FIG. 3.—Means of habitat and movement variables velocity, slope of movement, and percentage slope by hour-month intervals for elk (left column) and deer (right column). See Fig. 1 for additional explanation.

pography (Fig. 4B), and at increasing distance to streams (Fig. 4C). During afternoon hours, movements were directed toward steeper slopes (Fig. 3C) in valley landforms (Fig. 4B) as elk moved toward streams (Fig. 4C). Shift in habitat during daytime affected the dusk habitat transition (1700–2000 h), where movements were strongly upslope (Fig. 3B), out of drainages, to areas that are characteristic of foraging areas (lower canopy cover, greater distance to hiding cover, larger herbage, closer to roads, and more southerly and westerly aspects; Figs. 1A–C, 2A, 2B, and 4A).

Seasonal patterns for elk.—Amplitude and daily pattern of habitat use changed dramatically among monthly intervals for nearly all variables examined. Canopy, distance to hiding cover (Figs. 1A and 1B), and distance to open roads (Figs. 2B) changed across monthly intervals in both

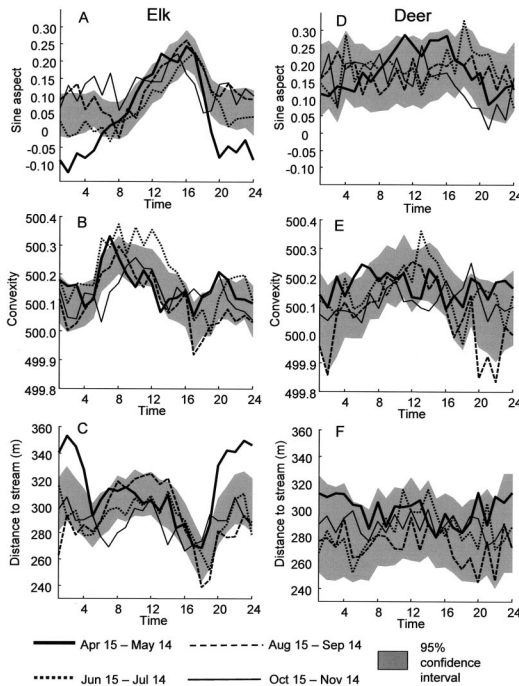


FIG. 4.—Means of habitat variables sine aspect, convexity, and distance to stream by hour-month intervals for elk (left column) and deer (right column). See Fig. 1 for additional explanation.

daily habitat amplitudes and intercepts. Overall use of canopy increased from the early intervals (15 April to 14 June) to mid-season (15 June to 14 August) and then decreased during daytime in the last monthly interval, 15 September to 14 October ($P < 0.05$, $d.f. = 354$). Seasonal differences were most evident for many other variables in the contrast between late spring (15 April to 14 June) and early summer (15 June to 14 August). For example, cosine aspect showed strong daily amplitudes in spring and autumn and remained constant throughout the day and night in midsummer (Fig. 1C). Across the 7 monthly intervals, amplitude of the crepuscular velocity peaks (Fig. 3A) was closely related to magnitude of daily habitat transitions. Crepuscular peaks in elk velocity were higher during monthly intervals 1 and 7, when elk used southerly and westerly aspects having low slopes, far

from water and roads, and low canopy. Both the crepuscular velocity peaks and crepuscular habitat transitions were dampened for the remaining intervals, especially interval 3 (15 June to 14 July).

Daily patterns for mule deer.—Regression models of individual deer daily cycles had lower r^2 values ($\bar{X} = 0.21$; range, 0.0–0.48) and fewer significant regression terms compared with elk (Table 4). High variation among animals and small changes in habitat use and movements contributed to low r^2 values. Distance to road, cosine of aspect, canopy, and velocity showed significant 24- or 12-h regression terms for most or all intervals (Table 4). Few of the 6- and 8-h regression terms were significant, except for velocity and cosine of aspect (Table 4).

Patterns of hourly habitat use and movements over the seven 1-month intervals showed that, relative to elk, deer used habitats on more southerly (Fig. 1F) and easterly aspects (Fig. 4D), with lower daytime canopy cover (Fig. 1D), closer to open roads (Fig. 2E), and with greater daytime herbage (Fig. 2D). More striking was the divergent pattern of daily habitat use between the 2 species, especially in the variables canopy cover, distance to hiding cover, cosine aspect, and herbage (Figs. 1A–F, 2A, and 2D). For distance to open road, patterns were similar between elk and mule deer, although daily amplitude was about one-third that observed for elk and variation was wider among the intervals (Figs. 2B and 2E). Convexity was the only other variable that exhibited a consistent daily cycle for deer (Fig. 4E). The weaker daily habitat amplitudes observed for deer were consistent with daily patterns in velocity (Fig. 3D). Deer velocities showed diminished crepuscular peaks that were about half (3.5 m/min) of those observed for elk (7 m/min). Deer velocities were extremely low during midday in summer and roughly equal to the estimated velocity of the stationary collars at Starkey (0.66 m/min) that exhibited a nonzero velocity resulting from telemetry error.

TABLE 4.—Significant ($P < 0.05$) regression terms for 24-, 12-, 8-, and 6-h sine and cosine functions for mule deer. Dates for intervals: 1, 15 April to 14 May; 3, 15 June to 14 July; 5, 15 August to 14 September; and 7, 15 October to 14 November. Abbreviations as in Table 3.

	Interval 1						Interval 3						Interval 5						Interval 7					
	24 h	12 h	8 h	6 h	r^2		24 h	12 h	8 h	6 h	r^2		24 h	12 h	8 h	6 h	r^2		24 h	12 h	8 h	6 h	r^2	
Canopy cover	C	S			0.36		C				0.26		C				0.19		S					0.15
Distance to hiding cover	C	S	S		0.40						0.14		C	C	C		0.21		S					0.22
Cosine aspect	C				0.21		C				0.17		C	S			0.28		B					0.25
Herbage					0.12						0.07		C	S			0.09		S					0.09
Distance to open road	C	S	C		0.45		C				0.18		B				0.32		C	C				0.28
Distance to closed road	C		C		0.30		C				0.18						0.19		C					0.18
Velocity				B	0.47		B	B	S		0.43		B	B	B	S	0.48		B	B	C			0.28
Slope of movement					0.04		B		S		0.04		S				0.11							0.00
Slope		C			0.31		C	C	C		0.18		C	C			0.19							0.19
Sine aspect	C				0.34			C			0.30				S		0.10		B	S				0.08
Convexity	S	S	S		0.16		C	C			0.14		C	S			0.08		S		S			0.10
Distance to stream		C			0.39		C	C			0.17		C	C			0.30							0.22

In contrast to changes in elk, we did not detect consistent daytime changes in habitat except that deer moved to areas of slightly higher convexity between 0600 and 1200 h (Fig. 4E). This weak trend was reversed between 1200 and 1700 h and proceeded at the same rate as in the morning hours, creating a symmetrical cycle of daytime habitat use. In addition, there was a weak trend for slope of movement, which decreased throughout the day and became negative at around noon (Fig. 3E), indicating down-slope movements.

Seasonal patterns for mule deer.—Deer exhibited pronounced changes among monthly intervals in overall habitat use for a number of variables, including canopy cover, cosine of aspect, and slope, despite weak daily patterns (Figs. 1D, 1F, and 3F). Two distinct daily patterns were evident, 1 for very early and late intervals and 1 for the midseasons, although the trends were weaker and with fewer significant differences. Daily cycles for canopy cover and cosine of aspect (Figs. 1D and 1F) were inverted between interval 1 and many of the other 6 intervals, indicating major shifts in daily cycles of habitat use in spring versus summer and autumn.

DISCUSSION

Our description of seasonal and daily cycles in female elk and mule deer complements previous studies of habitat use at Starkey (Coe et al. 2001; Johnson et al. 2000; Rowland et al. 2000) and elsewhere (Collins and Urness 1983; Collins et al. 1978; Green and Bear 1990; Irwin and Peek 1983; McCorquodale et al. 1986; Unsworth et al. 1998). Patterns of elk activity have been described as circadian cycles between foraging and secure resting habitats with crepuscular transitions (Collins et al. 1978; Craighead et al. 1973; Green and Bear 1990; Irwin and Peek 1983; Leckenby 1984). Our analysis quantifies the spatial component and temporal dynamics of these circadian cycles over a 7-month time period and shows movement patterns as well. Dai-

ly cycles of movement of female elk observed in this study generally agree with activity patterns described previously (Collins et al. 1978; Green and Bear 1990), although direct comparisons are not possible. We did not differentiate between movements for feeding and those of sustained traveling and could only infer that resting occurred at periods of low velocity. Furthermore, we treated our data as continuous variables rather than categorical (resting, feeding, and traveling) and present means across multiple animals. Earlier work (Collins et al. 1978; Green and Bear 1990; Kie et al. 1991) used direct observations or tip switches to categorize activities and report more detailed observations for individual animals.

In addition to crepuscular habitat transitions between foraging and resting areas, we detected daytime habitat shifts for both elk and mule deer. Elk exhibited a steady shift during daylight hours to more easterly aspects and late in the day moved downslope toward streams. Mule deer moved to areas on flatter slopes and to more southerly aspects. Low-velocity, daytime habitat shifts by elk were consistently observed among all intervals examined, although habitat variables like canopy and distance to roads remained relatively constant. We speculate that daytime habitat shifts are used by elk at Starkey to thermoregulate during midday on summer range (Collins and Urness 1983; Green and Bear 1990; Leckenby 1984; Lyon 1979; Millspaugh et al. 1998; Ockenfels and Brooks 1994; Zahn 1985). Cook et al. (1998) report that the use of cover by female elk to reduce heat loads may enhance comfort but does not improve animal performance as indicated by changes in body mass. However, the combined effects of topography and cover on animal energetic balances in elk have not been examined.

Seasonal changes in daily cycles for female elk and deer observed in this study and elsewhere (Collins and Urness 1983; Collins et al. 1978; Wallace and Krausman

1997) are likely driven by the phenology of primary forage species (Skovlin 1967). For instance, high daily amplitudes for velocity and habitat variables in spring (15 April to 14 May) and autumn (15 October to 14 November) reflect high search rates for specific meadows at Starkey that produce abundant forage in early spring and in autumn after the 1st substantial rains (Skovlin 1967). Meadows and grasslands provide the most efficient foraging for elk (Collins and Urness 1983; Wickstrom et al. 1984), especially in early spring, when overall forage is limited on summer range. The use of open meadows by deer at Starkey is largely confined to spring and early summer and creates daily patterns that are inverted as compared with the other monthly intervals. Use of these specific forage resources by both elk and deer results in sharp crepuscular habitat transitions, especially in aspect, canopy, and distance to road, all mediated via relatively high crepuscular velocities.

During midsummer (15 July to 14 August) elk showed markedly lower velocity and dampened daily cycles with respect to many habitat variables. Elk used forests with more canopy on more easterly and northerly aspects throughout the day and night. This change in cycles of habitat use is consistent with seasonal progression of forage abundance and quality at Starkey, where declining forage quality in the grasslands (Skovlin 1967) and high production under forest stands make the latter more preferred foraging areas later in summer (Edgerton and Smith 1971; Holechek et al. 1982; Unsworth et al. 1998). Increased use of forage resources under forest canopies had the net effect of dampening the crepuscular velocity peaks and daily amplitudes for many habitat variables as well. We speculate that the dramatic dampening of daily cycles of habitat use and velocity during midsummer (monthly interval 3) is also related to neonatal care of elk calves. At this time, elk calves at Starkey are between 2 and 6 weeks old (R. M. Stussy, in litt.) and

are just becoming mobile. Unsworth et al. (1998) observed shifts in habitat use by female elk during calving and suggested that these shifts were to minimize risk of calf predation.

Deer exhibited dampened daily cycles of movement and habitat transitions compared with elk and generally used habitats with higher forest canopy, with more easterly aspects, and closer to open roads. Collins and Urness (1983) also observed lower velocities for deer compared with elk, and Beier and McCullough (1990) observed low levels of activity for white-tailed deer (*Odocoileus virginianus*) during midsummer, when they used forested habitats with abundant forage. Smaller home ranges (Kie et al. 2002; Loft et al. 1993) and a foraging behavior that is better adapted to using shrub-dominated habitats or closed canopy forests can help explain the observed differences in habitat use between deer and elk.

The weak patterns of daily and seasonal habitat shifts we observed for deer also can be attributed to the scale of our telemetry and habitat data. Deer exhibit a higher frequency of feeding and resting cycles than elk (Hoffman 1985); thus, a higher frequency of sampling is required to detect alternating cycles of foraging and resting. Similarly, the spatial grain of cycles in habitat use for deer may be finer than what we can detect with the Starkey telemetry system. Small movements into foraging patches, for example, could be difficult to detect given that a mean 50-m telemetry error at Starkey could encompass an array of habitat types.

One apparent interspecific difference in daily cycles is that deer did not exhibit a daytime shift in aspects or move to more concave landforms (valley bottoms). Previous studies show that deer seek shady areas to reduce heat load during daytime in the summer (Beier and McCullough 1990; Collins and Urness 1983; Parker and Robbins 1984). Our data suggest that for midsummer periods midday canopy use was lower than nocturnal use. Combined, this

suggests that deer may well be exploiting areas of shade under the low-canopy forests, a situation that cannot be detected at the resolution of our vegetation and telemetry data. These midsummer patterns of habitat use by deer may have resulted from deer avoiding concentrations of elk (Johnson et al. 2000; Stewart et al. 2002).

Daily and seasonal dynamics of habitat use on summer range can strongly bias our perception of habitat quality for the 2 species. Many factors influence seasonal and daily patterns of habitat use as elk and deer meet daily metabolic requirements. Clearly, choice of a temporal scale for either sampling or stratifying data can significantly alter the observed patterns of habitat use. Our results can provide insights to temporal sampling strategies and optimal allocation of telemetry resources for future studies on elk and deer in western North America.

The dynamic nature of patterns of habitat use in elk and deer is difficult to reconcile with commonly used elk and deer habitat models (Thomas et al. 1988). For instance, the assumption that roads and associated disturbances are primary agents driving elk distributions across landscapes and seasons (Leege 1984; Lyon 1983) might be an oversimplification in the context of seasonal and daily patterns, particularly where road closures are expected to moderate the influences of roads on patterns of animal use.

The complex spatial and temporal patterns of habitat use by elk and deer complicate the spatial modeling of ungulate behavior as individuals or populations. The significance of the daily cycles and seasonal changes in these cycles is rarely discussed in modeling efforts (Gross et al. 1995; Hobbs 1996; Jorritmsa et al. 1999; Kienast 1999; Pastor and Naiman 1992; Putman 1996; Riggs et al. 2000; Turner et al. 1993). Modeling ungulates like deer that exhibit high-frequency cycles of habitat use and rapidly change their distributions in response to other ungulates poses a significant challenge. It was interesting to note that velocity consistently showed high r^2

values and small confidence intervals compared with habitat variables, meaning that the timing and magnitude of movements appear to be more consistent among animals than the choice of habitat type. In any case, animal-to-animal variation will complicate the validation of movement and habitat models on large landscapes. Clearly, the greatest challenge to modeling efforts will be the choice of an appropriate spatial and temporal scale that does not omit critical features of the daily and seasonal habitat use and movement cycles.

ACKNOWLEDGMENTS

We thank Starkey project personnel C. Borum, N. Cimon, P. Coe, B. Dick, R. Kennedy, J. Nothwang, J. Noyes, R. Stussy, M. Vavra, and M. Wisdom for assistance with this study. This research was funded by the United States Forest Service Pacific Northwest Research Station and Pacific Northwest Region and under provisions of the Federal Aid in Wildlife Restoration Act (Pittman–Robertson Act), administered by the Oregon Department of Fish and Wildlife. We thank M. Rowland, M. Wisdom, H. Preisler, and R. Riggs for their reviews of earlier drafts of the manuscript. Editorial assistance from L. Dillavou is gratefully acknowledged.

LITERATURE CITED

- BEIER, P., AND D. R. MCCULLOUGH. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:1–51.
- BRILLINGER, D. R., H. K. PREISLER, A. A. AGER, AND J. G. KIE. 2001. The use of potential functions in modeling animal movement. Pp. 369–386 in *Data analysis from statistical foundations* (A. K. Md. E. Saleh, ed.). Nova Science, New York.
- BRILLINGER, D. R., H. K. PREISLER, A. A. AGER, AND J. G. KIE. In press. An exploratory data analysis (EDA) of the paths of moving animals. *Journal of Statistical Planning and Inference*.
- BRILLINGER, D. R., H. K. PREISLER, A. A. AGER, J. G. KIE, AND B. S. STEWART. 2002. Employing stochastic differential equations to model wildlife motion. *Bulletin of the Brazilian Mathematical Society* 33:93–116.
- BRYANT, L. D., J. W. THOMAS, AND M. M. ROWLAND. 1993. Techniques to construct New Zealand elk-proof fence. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-313:1–17.
- COE, P. K., B. K. JOHNSON, J. W. KERN, S. L. FINDHOLT, J. G. KIE, AND M. J. WISDOM. 2001. Responses of elk and mule deer to cattle in summer. *Journal of Range Management* 54:205A51–A76.
- COLLINS, W. B., AND P. J. URNESS. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *Journal of Wildlife Management* 47:646–663.
- COLLINS, W. B., P. J. URNESS, AND D. D. AUSTIN. 1978. Elk diets and activities on different lodgepole pine habitat segments. *Journal of Wildlife Management* 42:799–810.
- COOK, J. G., L. L. IRWIN, L. D. BRYANT, R. A. RIGGS, AND J. W. THOMAS. 1998. Influence of forest cover on condition of elk in summer and winter. *Wildlife Monographs* 141:1–61.
- CRAIGHEAD, J. J., F. C. CRAIGHEAD, JR., R. L. RUFF, AND B. W. O'GARA. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison drainage herd as determined by biotelemetry. *Wildlife Monographs* 33:1–50.
- DANA, P. H., W. FOWLER, AND D. HINDMAN. 1989. Automated animal-tracking system: tracking elk with retransmitted Loran-C. Pp. 53–61 in *Proceedings of the 18th annual technical symposium of the International Loran Association* (J. M. Beukers, ed.). International Loran Association, Santa Barbara, California.
- DIGGLE, P. J. 1990. Time series: a biostatistical introduction. Oxford statistical science series 5. Oxford Science Publications, Oxford University Press, New York.
- EDGERTON, P. J., AND J. G. SMITH. 1971. Seasonal forage use by deer and elk on the Starkey Experimental Forest and Range, Oregon. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Research Paper PNW-112:1–12.
- FINDHOLT, S. L., B. K. JOHNSON, L. D. BRYANT, AND J. W. THOMAS. 1996. Corrections for position bias of a Loran-C radio telemetry system using DGPS. *Northwest Science* 70:273–280.
- FOCARDI, S., P. MARCELLINI, AND P. MONTANARO. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *Journal of Applied Ecology* 65:606–620.
- GREEN, R. A., AND G. D. BEAR. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. *Journal of Wildlife Management* 54:272–279.
- GROSS, J. E., C. ZANK, N. T. HOBBS, AND D. E. SPALLINGER. 1995. Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. *Landscape Ecology* 10:209–217.
- HOBBS, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- HOFFMAN, R. R. 1985. Digestive physiology of the deer: their morphophysiological specialisation and adaptation. Pp. 393–407 in *Biology of deer production* (P. F. Fennessy and K. R. Drew, eds.). Royal Society of New Zealand, Wellington, New Zealand.
- HOLECHEK, J. L., M. VAVRA, J. SKOVLIN, AND W. C. KRUEGER. 1982. Cattle diets in the Blue Mountains of Oregon II. Forests. *Journal of Range Management* 35:239–242.
- IRWIN, L. L., AND J. M. PEEK. 1983. Elk habitat use

- relative to forest succession in Idaho. *Journal of Wildlife Management* 47:664–672.
- JOHNSON, B. K., A. A. AGER, S. CRIM, M. J. WISDOM, S. L. FINDHOLT, AND D. SHEEHY. 1996. Allocating forage among wild and domestic ungulates—a new approach. Pp. 166–168 in *Proceedings on sustaining rangeland ecosystems* (W. D. Edge and S. L. Olson-Edge, eds.). Oregon State University, Corvallis.
- JOHNSON, B. K., J. W. KERN, M. J. WISDOM, S. L. FINDHOLT, AND J. G. KIE. 2000. Resource selection and spatial separation of elk and mule deer in spring. *Journal of Wildlife Management* 64:685–697.
- JOHNSON, B. K., ET AL. 1998. Mitigating spatial differences in observation rate of automated telemetry systems. *Journal of Wildlife Management* 62:958–967.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- JORRITMSA, I. T. M., A. F. M. VAN HEES, G. M. J. MOHRENN. 1999. Forest development in relation to ungulate grazing: a modeling approach. *Forest Ecology and Management* 120:23–34.
- KAY, C. E., AND D. L. BARTOS. 2000. Ungulate herbivory on Utah aspen. Assessment of long-term exclosures. *Journal of Range Management* 53:145–153.
- KIE, J. G., R. T. BOWYER, B. B. BOROSKI, M. C. NICHOLSON, AND E. R. LOFT. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83:530–544.
- KIE, J. G., C. J. EVANS, E. R. LOFT, AND J. W. MENKE. 1991. Foraging behavior by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55:665–674.
- KIENAST, F., J. FRITSCHI, M. BISSEGGER, AND W. ABDERHALDEN. 1999. Modeling successional patterns of high-elevation forests under changing herbivore pressure—responses at the landscape level. *Forest Ecology and Management* 120:35–46.
- LECKENBY, D. A. 1984. Elk use and availability of cover and forage habitat components in the Blue Mountains, northeast Oregon, 1976–1982. Oregon Department of Fish and Wildlife, Wildlife Research Report 14:1–40.
- LEEGE, T. A. (COMPILER). 1984. Guidelines for evaluating and managing summer elk habitat in northern Idaho. Idaho Department of Fish and Game, Wildlife Bulletin 11:1–37.
- LOFT, E. R., J. G. KIE, AND J. W. MENKE. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. *California Fish and Game* 79:145–166.
- LYON, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *Journal of Forestry* 79:658–660.
- LYON, L. J. 1983. Road density models describing habitat effectiveness models for elk. *Journal of Forestry* 81:592–595.
- MACKIE, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. *Wildlife Monographs* 20:1–79.
- MCCORQUODALE, S. M., K. J. RAEDEKE, AND R. D. TÄBER. 1986. Elk habitat use patterns in the shrub steppe of Washington. *Journal of Wildlife Management* 50:664–669.
- MILLSPAUGH, J. J., K. J. RAEDEKE, G. C. BRUNDIGE, AND C. C. WILLMOTT. 1998. Summer bed sites of elk (*Cervus elaphus*) in the Black Hills of South Dakota: considerations for thermal cover management. *American Midland Naturalist* 139:133–140.
- MORRIS, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology* 6:412–432.
- NOYES, J. H., B. K. JOHNSON, L. D. BRYANT, S. L. FINDHOLT, AND J. W. THOMAS. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. *Journal of Wildlife Management* 60:508–527.
- OCKENFELS, R. A., AND D. E. BROOKS. 1994. Summer diurnal bed sites of Coues white-tailed deer. *Journal of Wildlife Management* 58:70–75.
- OTIS, D. L., AND G. C. WHITE. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63:1039–1044.
- PARKER, K. L., AND C. T. ROBBINS. 1984. Thermoregulation in mule deer and elk. *Canadian Journal of Zoology* 62:1409–1422.
- PASTOR, J., AND R. J. NAIMAN. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690–705.
- PUTMAN, R. J. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman & Hall, London, United Kingdom.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RIGGS, R. A., ET AL. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Research Paper PNW-527:1–77.
- ROWLAND, M. M., L. D. BRYANT, B. K. JOHNSON, J. H. NOYES, M. J. WISDOM, AND J. W. THOMAS. 1997. The Starkey project: history, facilities, and data collection methods for ungulate research. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-396:1–62.
- ROWLAND, M. M., M. J. WISDOM, B. K. JOHNSON, AND J. G. KIE. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64:672–685.
- ROWLAND, M. M., ET AL. 1998. The Starkey habitat database for ungulate research: construction, documentation, and use. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-430:1–48.
- SAS INSTITUTE INC. 1994. SAS user's guide: statistics. Version 6.10. SAS Institute Inc., Cary, North Carolina.
- SKOVLIN, J. M. 1967. Fluctuations in forage quality on summer range in the Blue Mountains. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Research Paper PNW-44:1–20.
- STEWART, K. M., T. M. BOWYER, J. G. KIE, N. CIMON, AND B. K. JOHNSON. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource parti-

- tioning and competitive displacement. *Journal of Mammalogy* 83:229–244.
- THOMAS, J. W., D. A. LECKENBY, M. HENJUM, R. J. PEDERSEN, AND L. D. BRYANT. 1988. Habitat effectiveness index for elk on Blue Mountain winter ranges. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-218:1–28.
- TURNER, M. G., Y. WU, W. H. ROMME, AND L. L. WALLACE. 1993. A landscape simulation model of winter foraging by large ungulates. *Ecological Modeling* 69:163–184.
- UNSWORTH, J. W., L. KUCK, E. O. GARTON, AND B. B. BUTTERFIELD. 1998. Elk habitat selection on the Clearwater national forest, Idaho. *Journal of Wildlife Management* 62:1255–1263.
- WALLACE, M. C., AND P. R. KRAUSMAN. 1997. Movements and home-ranges of elk in eastern Arizona. Pp. 184–185 in *Proceedings of the 1997 deer and elk workshop* (J. C. deVos, Jr., ed.), Rio Rico, Arizona. Arizona Department of Game and Fish, Phoenix.
- WICKSTROM, M. L., C. T. ROBBINS, T. A. HANLEY, D. E. SPALINGER, AND S. M. PARISH. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285–1301.
- WISDOM, M. J., J. G. COOK, M. M. ROWLAND, AND J. H. NOYES. 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-311:1–49.
- ZAHN, H. M. 1985. Use of thermal cover by elk (*Cervus elaphus*) on a western Washington summer range. Ph.D. dissertation, University of Washington, Seattle.
- Submitted 12 June 2002. Accepted 8 November 2002.*
- Associate Editor was Ronald E. Barry.*